

# Gibberellic acid in plant

## Still a mystery unresolved

Ramwant Gupta\* and S K Chakrabarty

Division of Seed Science and Technology; Indian Agricultural Research Institute; New Delhi, India

**Keywords:** gibberellic acid, seed germination, dormancy, sex expression

Gibberellic acid (GA), a plant hormone stimulating plant growth and development, is a tetracyclic di-terpenoid compound. GAs stimulate seed germination, trigger transitions from meristem to shoot growth, juvenile to adult leaf stage, vegetative to flowering, determines sex expression and grain development along with an interaction of different environmental factors viz., light, temperature and water. The major site of bioactive GA is stamens that influence male flower production and pedicel growth. However, this opens up the question of how female flowers regulate growth and development, since regulatory mechanisms/organs other than those in male flowers are mandatory. Although GAs are thought to act occasionally like paracrine signals do, it is still a mystery to understand the GA biosynthesis and its movement. It has not yet confirmed the appropriate site of bioactive GA in plants or which tissues targeted by bioactive GAs to initiate their action. Presently, it is a great challenge for scientific community to understand the appropriate mechanism of GA movement in plant's growth, floral development, sex expression, grain development and seed germination. The appropriate elucidation of GA transport mechanism is essential for the survival of plant species and successful crop production.

### History and Evolution

Gibberellins commonly known as gibberellic acids first came to the attention of western scientists in 1950s, they had been discovered much earlier in Japan. Rice farmers of Japan had long known of a fungal disease called foolish seedling or *bakanae* disease in Japanese that causes rice plants to grow taller and eliminated seed production. Plant pathologists found that these symptoms in rice plant were induced by a chemical secreted by a pathogenic fungus, *Gibberella fujikuroi*. Culturing this fungus in the laboratory and analyzing the culture filtrate enabled Japanese scientists in the 1930s to obtain impure crystal of two fungal "compounds" possessing plant growth promoting activity. One of these, because it was isolated from the fungus *Gibberella*, was named gibberellin A. In 1950s scientists of Tokyo University separated and characterized 3 different gibberellins from

gibberellin A sample, and named them gibberellin A<sub>1</sub>, gibberellin A<sub>2</sub> and gibberellin A<sub>3</sub>. The numbering system for gibberellins used in the past 50 y builds on this initial nomenclature of gibberellins A<sub>1</sub> (GA<sub>1</sub>), GA<sub>2</sub>, and GA<sub>3</sub>.

In the same year, 2 research groups, one at Imperial Chemical Industries in Britain and other at the US Department of Agriculture (USDA) in Illinois, elucidated the chemical structure of the compound that they had purified from *Gibberella* culture filtration and named gibberellic acid. This compound was later shown to be identical to the gibberellin isolated by the Japanese scientist. For this GA<sub>3</sub> is also referred to as gibberellic acid. GA<sub>3</sub> is the principal component in *Gibberella* culture. The GA<sub>3</sub> is the most frequently produced GA in commercial industrial scale fermentations of *Gibberella* for agronomic, horticultural and other scientific uses. Identification of a GA from a plant extract was first made in 1958 with the discovery of GA<sub>1</sub> from immature seeds of vuner bean (*Phaseolus cocineus*). As more and more GAs from *Gibberella* and different plant sources were characterized, a scheme was adopted in 1968 to number them (GA<sub>1</sub>–GA<sub>4</sub>), in chronological order of their discovery.

### Gibberellin Biosynthesis

Gibberellins (GAs) are endogenous plant growth regulators, having tetracyclic, diterpenoid compounds. After valuable efforts to understand the GA biosynthesis and movements, the appropriate site of bioactive GA in plants or tissues targeted by bioactive GAs to initiate their action has not yet been confirmed. Dwarf plant bioassay and its quantitative analysis revealed the presence of GA in active growing tissues i.e., shoot apices, young leaves and flowers.<sup>1,2,3</sup> In contrast, there are some reports for the presence of GAs in xylem and phloem exudates, indicating a long-distance transport of Gas.<sup>4,5</sup> The transport of active GAs and their intermediates was supported by grafting experiments.<sup>6,7,8</sup> The contradictory results obtained from different experiments could not pin-point the site of synthesis of bioactive GA. Gibberellins being synthesized via the terpenoid pathway, require 3 enzymes viz., terpene synthase (TPSs), cytochrome P450 mono-oxygenase (P450s) and 2-oxoglutarate dependent dehydrogenase (2 ODDs), for the biosynthesis of bioactive

Correspondence to: Ramwant Gupta; Email: ramwantgupta@yahoo.com

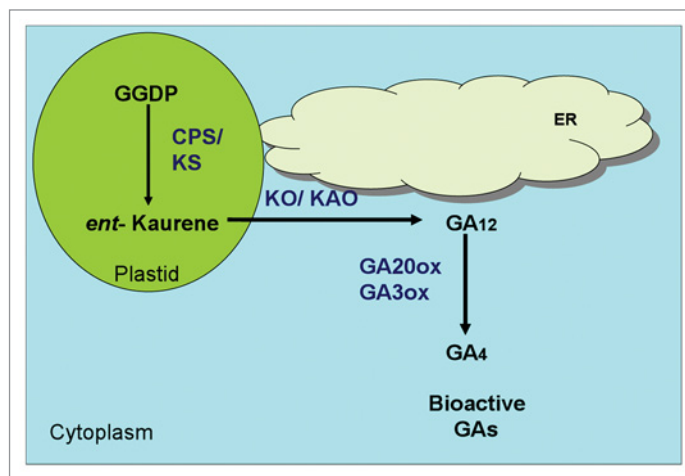
Submitted: 04/30/13; Revised: 06/21/13; Accepted: 06/22/13

Citation: Gupta R, Chakrabarty SK. Gibberellic acid in plant: Still a mystery unresolved. Plant Signal Behav 2013; 8: e25504; <http://dx.doi.org/10.4161/psb.25504>

GA from GGDP in plants (Fig. 1). Two terpene synthase, *ent*-copalyl diphosphate synthase (CPS) and *ent*-kaurene synthase (KS), located in plastids, involved in conversion of GGDP to tetracyclic hydrocarbon intermediate *ent*-kaurene (Fig. 1).<sup>9,10,11</sup> *ent*-Kaurene is then converted to GA<sub>12</sub> by 2 P450s. First, *ent*-Kaurene oxidase (KO) present in the outer membrane of plastid,<sup>12</sup> catalyzes the sequential oxidation on C-19 to produce *ent*-kaurenoic acid. Second, *ent* kaurenoic acid oxidase (KAO) present in endoplasmic reticulum is subsequently converted to GA<sub>12</sub>.<sup>12,13</sup> Bioactive GA<sub>4</sub> is converted from GA<sub>12</sub> through oxidations on C-20 and C-3 by GA 20-oxidase (GA20ox) and GA 3-oxidase (GA3ox), respectively (Fig. 1).

### GA Signaling in Dormancy and Seed Germination

Seed contains embryo that is arrested to develop in to plant with appropriate environmental conditions to continue their life cycles.<sup>14</sup> Breaking of seed dormancy to germination is controlled by some physical factors (light, temperature and moisture) and by the endogenous growth regulating hormones (GA and ABA). GA stimulates the seed germination whereas, ABA is involved in the establishment and maintenance of dormancy.<sup>15</sup> GA exerts its influence in two manners, first by increasing the growth potential of embryo and second by inducing hydrolytic enzymes.<sup>16,17,18</sup> During seed germination embryonic GA is released that triggers the weakness of seed cover by stimulating gene expression involved in cell expansion and modification as reported in *Arabidopsis*.<sup>19</sup> GAs represent a natural regulator of the processes involved in seed germination to stimulate the production of hydrolytic enzyme i.e.,  $\alpha$ -amylase, in the aleurone layer of germinating cereal grains.<sup>20,21</sup> Cereal grains can be divided into 3 parts i.e., embryo, endosperm and seed coat. The endosperm is composed of the aleurone layer and centrally located starchy endosperm. The starchy endosperm, typically non-living at maturity, consists of thin walled cells with starch grains surrounded by aleurone layer, having thick cell wall with protein bodies. As consequences, the stored food reserves of the starchy endosperms are broken down into soluble sugars, amino acids, and other products that are transported to the growing embryo. GA biosynthetic enzymes, GA 20-oxidase and GA 3-oxidase genes show tissue and cell specific patterns of expression in germinating grain of rice,<sup>22</sup> although this expression is confined to the epithelium and developing shoot tissues of germinating embryo. The embryo seems to be a site of GA biosynthesis and response, whereas aleurone layer shows site of response only. The response is not same in both the locations. In the aleurone, synthesis of  $\alpha$ -amylase takes place, whereas in developing shoot cell division/elongation. The expression of  $\alpha$ -amylase gene is upregulated by exogenous GA, mediated through SLN1 and GAMYB transcription factors.<sup>23</sup> On the other hand, PKABA1, an ABA-responsive serine/threonine protein kinase, inhibits gene expression in barley.<sup>24</sup> GA not only restricts to the secretion of hydrolytic enzymes but, trigger the programmed cell death, combining with reactive oxygen species. The aleurone gene expression pattern has identified many new genes whose regulation is up/downregulated by GA and ABA treatment in barley. Mutation in a gene encoding



**Figure 1.** Gibberellins biosynthesis pathway; residing in 3 different cellular compartments (plastid, endoplasmic reticulum and cytoplasm). GGDP, geranylgeranyl diphosphate; *ent*-CDP, *ent*-copalyl diphosphate; CPS, *ent*-copalyl diphosphate synthase; KS, *ent*-kaurene synthase; KO, *ent*-kaurene oxidase; KAO, *ent*-kaurenoic acid oxidase.

a hetero-trimeric GA protein impairs GA signaling in aleurone cells causes dwarf phenotype in rice.<sup>25</sup> Radical emergence requires breaking the endosperm caps, a major physical restraint to germination in tomato and tobacco. The *GA-deficient-1* (*gib-1*) mutant of tomato and *Arabidopsis gal-3* mutant could not germinate without exogenous GA application, however it germinated when endosperm caps were removed.<sup>26</sup> GA plays an important role in the endosperm cap weakening. The bioactive GAs are produced in embryo and transported to aleurone layer,<sup>27</sup> and trigger the expression of  $\alpha$ -amylase<sup>28</sup> was confirmed after physiological and biochemical characterization. It is concluded that during seed germination the aleurone layer is unable to synthesize GA but perceive the GA signals.

### GA Biosynthesis and Signaling in the Apical Meristem

Physiological studies and phenotypic characterization of mutants with impaired GA biosynthesis revealed that GA plays an important role in internode elongation.<sup>29,30,31</sup> It stimulates cell division and expansion in response to light or dark (photomorphogenesis and skoto-morphogenesis).<sup>16,32,33,34,35</sup> Despite complexity, the GA biosynthetic pathway has been well characterized.<sup>36</sup> It is very difficult to determine precisely the site of bioactive GA biosynthesis in plants. Very little is known about level of GA in plants and still much remain to understand the signal transduction pathways leading to elongation of stems and leaves with response to different environmental factors. Various studies on gene expression and characterization of GA deficient mutants revealed GA signaling and bioactive sites in plants.<sup>37,38</sup> A model proposed by Sakamoto<sup>39</sup> depicted relationship between GA biosynthesis and cell fate determination at the apical region of tobacco shoot. A KNOTTED1-like homeobox (KNOX) protein, NTH15 is present at the corpus region of the shoot apical meristem (SAM). An interaction with the cis-acting

element results a negative regulation of the GA 20-oxidase gene. When NTH15 expression is controlled, GA biosynthesis starts and finally stimulates cell division and determines cell fate. In rice, the expression of GA related genes is restricted to the basal and peripheral region of the SAM rather than corpus region.<sup>40</sup> In rice corpus region of SAM expressed OSH1 and KNOX type homeobox genes to determine cell fate.<sup>41</sup> Another report also revealed the expression of GA regulated genes in growing tissues of *Arabidopsis*.<sup>42</sup> GA promotes cell elongation through releasing DELLA mediated inhibition of BZR1 transcription factor.<sup>43</sup>

### GA in the Flowering and Sex Expression

GAs regulates flower initiation and its development and it is essential for male and female fertility not for differentiation of floral organs.<sup>44</sup> GA-deficient mutants in *Arabidopsis* and tomato showed abnormal stamen development,<sup>45,46,47</sup> while extreme GA deficiency revealed female sterility.<sup>48,49</sup> No viable pollen develops in severe GA-deficient mutants, and sepals, petals, and pistils are underdeveloped, leading in some cases even to premature abortion of the flower.<sup>48,49,50</sup> Application of bioactive GAs or even of the GA precursor GA9 restores normal flower development. *Arabidopsis* stamens require higher GA concentration than do the other floral Organs,<sup>49</sup> stamens offer a rich source for GAs, as has been demonstrated in rice.<sup>51</sup> Moreover, for a long time it has been known that in *Glechoma hederacea*, stamen-derived GAs stimulate corolla growth.<sup>52</sup> Griffiths<sup>44</sup> found that not only the stamen and petal development arrested and the pistil length reduced, but also reduced the pedicel elongation in triple GID1 receptor mutants of *Arabidopsis*. Further, Hu et al.<sup>46</sup> identified stamens and/or flower receptacles as 2 potential sites for bioactive GA synthesis in *Arabidopsis* flowers, and suggest that GAs are transported from these organs to promote petal growth. GA-deficit mutants produced short stamen, resulting shortening in filaments and compromised self-pollination.<sup>53</sup> The tapetum, essential for pollen development providing nutrients, contains pollen coat and allowing dehiscence.<sup>54,55</sup> The tapetum seems to be a major site of GA biosynthesis in developing anthers in rice and *Arabidopsis*.<sup>22,46,56</sup> The expression of GA genes was reported in anthers only after meiosis<sup>45</sup> and it is interesting to speculate on the extent and distance GAs are exported from anthers.<sup>51</sup> GA plays very important role in pollen germination and pollen tube growth.<sup>45,57</sup> Pollens in GA deficit mutants do not germinate unless rescued by exogenous GA.<sup>45</sup> Late stamen development (filament elongation, anther dehiscence, and pollen maturation) regulated through GA in coordination with jasmonic acid, whereas the GA alone mediated early anther development.<sup>58</sup>

GA in pollen itself increases (7-fold) during pollen tube growth, but this may be species specific. Pollen is a rich source of GA and its content may be 200 fold greater than that in the ovary tissue both in *Petunia hybrida* and *Lillium*.<sup>59</sup> However, this level of pollen GA contributes little to total ovary GA at the time of pollination. Within hour of its germination, pollens' GA activity decrease drastically in *Petunia* and *Lilium*. Later in germination pollen tube growth becomes slow, and this might be reflected in decrease in bioactive GAs at this time, especially in angiosperm

pollen.<sup>60</sup> However, too little is known about differences in the timing of these changes during pollen tube growth on GA conversion, and in native GA type. Gibberellin is also reported to control sex expression by plant growth regulators. In cucumber GA3 treatments promote the male tendency in both gynocious and hermaphroditic lines.<sup>61,62</sup> Self-pollination study of female cucumber lines responded to repeated GA3 treatment to such an extent that the continuous female phase could be prevented.<sup>63</sup> There are indication that GA do not directly promote stamen differentiation in the embryonal floral bud but merely suppress female flower formation and that, in the lack of the latter, male flower ultimately develop.<sup>64</sup> However, in bitter melon GA3 at lower concentration promoted induction of female flowers and improved the fruit quality.<sup>65</sup> The highest number of female flowers per vine was recorded in bitter melon with 50 ppm GA3.<sup>66</sup> It also stimulates the pistillate flower development in castor bean, corn and hyoscyamus.<sup>60</sup>

### GA in Embryo Development

Gibberellins (GAs) are important constituent to regulate the temporal organization of maturation phase in maize.<sup>67</sup> Early embryogenesis in maize accumulated more bioactive GAs and the concentration decline as ABA level rises. Similar relationship between GA and ABA was reported in barley and wheat.<sup>68</sup> GA and ABA being antagonistic to each other maintain the relation between vivipary and quiescence; occur at or before stage 2 of embryo development.<sup>67</sup> However, the level at which gene expression is affected by GA modulation remains to be determined.

### Conclusion

Seed germination, stem elongation, meristematic tissue development and differentiation of floral organs are highly dependent on GA signaling system and mechanism. GA is required to break seed dormancy leading to its germination. Seed germination is a complex process, controlled by both physical and internal regulating factors. GA plays very important role in controlling and promoting germination in cereal grains and other crop species. It is confirmed that GA deficit mutants failed to germinate in absence of exogenous GA. However, a very small known GA signaling factors has been shown to mediate the regulation of seed germination. Physiological studies and phenotypic characterization of mutants impaired GA biosynthesis. It revealed that GA plays an important role in stem or internode elongation. It stimulates cell division and expansion in response to light or dark. GAs regulate flower initiation in some LD and biennial species and inhibit flowering of some perennials, and its development and it is essential for male and female fertility but not for the specification and differentiation of floral organs. GA3 treatment promotes the male tendency in both gynocious and hermaphroditic lines in some species. Three major points that are involved in the GA signaling mechanism are: 1) the stamen is the essential site of GA synthesis, other sites cannot replace the stamen; 2) GA20ox and GA3ox are



key regulators of GA biosynthesis in the stamen; and 3) short-distance movement of bioactive GA (but not of its biosynthetic precursors) from the stamen to the other floral organs and the pedicel is essential and sufficient for flower development. Thus, the stamen is the site that regulates, via bioactive GA, the male flower and the pedicel growth. However, this opens up the question of how female flowers regulate growth and development, since regulatory mechanisms/organs other than those in male flowers are mandatory. Although GAs are thought to act occasionally like paracrine signals do, but it is still a mystery to understand the exact mechanism of gibberellic acid

movement/transport in plants. Presently, it is a challenge for scientific community to understand the appropriate molecular mechanism of GA movement in plant's cell. It is still a mystery to understand the exact mechanism of gibberellic acid in plant growth, floral development, sex expression, grain development and seed germination. The appropriate elucidation of GA transport mechanism is essential for the survival of plant species and successful crop production.

#### Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

#### References

- Jones RL, Phillips ID. Organs of gibberellin synthesis in light-grown sunflower plants. *Plant Physiol* 1966; 41:1381-6; PMID:16656408; <http://dx.doi.org/10.1104/pp.41.8.1381>
- Kobayashi M, Yamaguchi I, Murofushi N, Ota Y, Takahashi N. Fluctuation and localization of endogenous gibberellins in rice. *Agric Biol Chem* 1988; 52:1189-94; <http://dx.doi.org/10.1271/bbb1961.52.1189>
- Potts WC. Internode length in *Pisum*. I. The effect of the *Le* gene difference on endogenous gibberellin-like substances. *Physiol Plant* 1982; 55:323-8; <http://dx.doi.org/10.1111/j.1399-3054.1982.tb00299.x>
- Hoad GV. Transport of hormones in the phloem of higher plants. *Plant Growth Regul* 1995; 16:173-82; <http://dx.doi.org/10.1007/BF00029538>
- Lang A. Gibberellins: structure and metabolism. *Annu Rev Plant Physiol* 1970; 21:537-70; <http://dx.doi.org/10.1146/annurev.pp.21.060170.002541>
- Katsumi M, Foard DE, Phinney BO. Evidence for the translocation of gibberellin A3 and gibberellin-like substances in grafts between normal, dwarf1 and dwarf 5 seedlings of *Zea mays* L. *Plant Cell Physiol* 1983; 24:379-88
- Proebsting WM, Hedden P, Lewis MJ, Croker SJ, Proebsting LN. Gibberellin concentration and transport in genetic lines of pea: effects of grafting. *Plant Physiol* 1992; 100:1354-60; PMID:16653128; <http://dx.doi.org/10.1104/pp.100.3.1354>
- Reid JB, Murfet IC, Potts WC. Internode length in *Pisum*. II. Additional information on the relationship and action of loci *Le*, *La*, *Cry*, *Na*, and *Lm*. *J Exp Bot* 1983; 34:349-64; <http://dx.doi.org/10.1093/jxb/34.3.349>
- Aach H, Bode H, Robinson DG, Graebe JE. ent-Kaurene synthetase is located in proplastids of meristematic shoot tissues. *Planta* 1997; 202:211-9; <http://dx.doi.org/10.1007/s004250050121>
- Sun TP, Kamiya Y. Regulation and cellular localization of ent-kaurene synthesis. *Physiol Plant* 1997; 101:701-8; <http://dx.doi.org/10.1111/j.1399-3054.1997.tb01054.x>
- Helliwell CA, Chandler PM, Poole A, Dennis ES, Peacock WJ. The CYP88A cytochrome P450, ent-kaurenoic acid oxidase, catalyzes three steps of the gibberellin biosynthesis pathway. *Proc Natl Acad Sci USA* 2001a; 98:2065-70; PMID:11172076; <http://dx.doi.org/10.1073/pnas.98.4.2065>
- Nelson DR, Schuler MA, Paquette SM, Werck-Reichhart D, Bak S. Comparative genomics of rice and *Arabidopsis*. Analysis of 727 cytochrome P450 genes and pseudogenes from a monocot and a dicot. *Plant Physiol* 2004; 135:756-72; PMID:15208422; <http://dx.doi.org/10.1104/pp.104.039826>
- Helliwell CA, Sullivan JA, Mould RM, Gray JC, Peacock WJ, Dennis ES. A plastid envelope location of *Arabidopsis* ent-kaurene oxidase links the plastid and endoplasmic reticulum steps of the gibberellin biosynthesis pathway. *Plant J* 2001b; 28:201-8; PMID:11722763; <http://dx.doi.org/10.1046/j.1365-313X.2001.01150.x>
- Bewley JD. Seed Germination and Dormancy. *Plant Cell* 1997; 9:1055-66; PMID:12237375; <http://dx.doi.org/10.1105/tpc.9.7.1055>
- Debeaujon I, Koornneef M. Gibberellin requirement for *Arabidopsis* seed germination is determined both by testa characteristics and embryonic abscisic acid. *Plant Physiol* 2000; 122:415-24; PMID:10677434; <http://dx.doi.org/10.1104/pp.122.2.415>
- Ogawa M, Hanada A, Yamauchi Y, Kuwahara A, Kamiya Y, Yamaguchi S. Gibberellin biosynthesis and response during *Arabidopsis* seed germination. *Plant Cell* 2003; 15:1591-604; PMID:12837949; <http://dx.doi.org/10.1105/tpc.011650>
- Kucera B, Cohn MA, Leubner-Metzger G. Plant hormone interactions during seed dormancy release and germination. *Seed Sci Res* 2005; 15:281-307; <http://dx.doi.org/10.1079/SSR2005218>
- Finch-Savage WE, Leubner-Metzger G. Seed dormancy and the control of germination. *New Phytol* 2006; 171:501-23; PMID:16866955; <http://dx.doi.org/10.1111/j.1469-8137.2006.01787.x>
- Finkelstein R, Reeves W, Ariizumi T, Steber C. Molecular aspects of seed dormancy. *Annu Rev Plant Biol* 2008; 59:387-415; PMID:18257711; <http://dx.doi.org/10.1146/annurev.arplant.59.032607.092740>
- Yamauchi Y, Ogawa M, Kuwahara A, Hanada A, Kamiya Y, Yamaguchi S. Activation of gibberellin biosynthesis and response pathways by low temperature during imbibition of *Arabidopsis thaliana* seeds. *Plant Cell* 2004; 16:367-78; PMID:14729916; <http://dx.doi.org/10.1105/tpc.018143>
- Seo M, Nambara E, Choi G, Yamaguchi S. Interaction of light and hormone signals in germinating seeds. *Plant Mol Biol* 2009; 69:463-72; PMID:19031046; <http://dx.doi.org/10.1007/s11103-008-9429-y>
- Kaneko M, Itoh H, Inukai Y, Sakamoto T, Ueguchi-Tanaka M, Ashikari M, et al. Where do gibberellin biosynthesis and gibberellin signaling occur in rice plants? *Plant J* 2003; 35:104-15; PMID:12834406; <http://dx.doi.org/10.1046/j.1365-313X.2003.01780.x>
- Gubler F, Chandler PM, White RG, Llewellyn DJ, Jacobsen JV. Gibberellin signaling in barley aleurone cells. Control of *SLN1* and *GAMYB* expression. *Plant Physiol* 2002; 129:191-200; PMID:12011350; <http://dx.doi.org/10.1104/pp.010918>
- Gómez-Cadenas A, Zentella R, Walker-Simmons MK, Ho THD. Gibberellin/abscisic acid antagonism in barley aleurone cells: site of action of the protein kinase PKABA1 in relation to gibberellin signaling molecules. *Plant Cell* 2001; 13:667-79; PMID:11251104
- Ueguchi-Tanaka M, Fujisawa Y, Kobayashi M, Ashikari M, Iwasaki Y, Kitano H, et al. Rice dwarf mutant d1, which is defective in the alpha subunit of the heterotrimeric G protein, affects gibberellin signal transduction. *Proc Natl Acad Sci USA* 2000; 97:11638-43; PMID:11027362; <http://dx.doi.org/10.1073/pnas.97.21.11638>
- Groot SPC, Karssen CM. Gibberellins regulate seed germination in tomato by endosperm weakening: A study with gibberellin-deficient mutants. *Planta* 1987; 171:525-31; <http://dx.doi.org/10.1007/BF00392302>
- Fincher GB. Molecular and cellular biology associated with endosperm mobilization in germinating cereal grains. *Annu Rev Plant Physiol Plant Mol Biol* 1989; 40:305-346; <http://dx.doi.org/10.1146/annurev.pp.40.060189.001513>
- Gubler F, Kalla R, Roberts JK, Jacobsen JV. Gibberellin-regulated expression of a myb gene in barley aleurone cells: evidence for Myb transactivation of a high-pI alpha-amylase gene promoter. *Plant Cell* 1995; 7:1879-91; PMID:8535141
- Hooley R. Gibberellins: perception, transduction and responses. *Plant Mol Biol* 1994; 26:1529-55; PMID:7858203; <http://dx.doi.org/10.1007/BF00016489>
- Swain SM, Olszewski NE. Genetic analysis of gibberellin signal transduction. *Plant Physiol* 1996; 112:11-7; PMID:12226370
- Ross JJ, Murfet IC, Reid JB. Gibberellin mutants. *Physiol Plant* 1997; 100:550-60; <http://dx.doi.org/10.1111/j.1399-3054.1997.tb03060.x>
- Alabadí D, Gallego-Bartolomé J, Orlando L, García-Cárcel L, Rubio V, Martínez C, et al. Gibberellins modulate light signaling pathways to prevent *Arabidopsis* seedling de-etiolation in darkness. *Plant J* 2008; 53:324-35; PMID:18053005; <http://dx.doi.org/10.1111/j.1365-313X.2007.03346.x>
- Feng S, Martínez C, Gusmaroli G, Wang Y, Zhou J, Wang F, et al. Coordinated regulation of *Arabidopsis thaliana* development by light and gibberellins. *Nature* 2008; 451:475-9; PMID:18216856; <http://dx.doi.org/10.1038/nature06448>
- de Lucas M, Davière JM, Rodríguez-Falcón M, Pontin M, Iglesias-Pedraz JM, Lorrain S, et al. A molecular framework for light and gibberellin control of cell elongation. *Nature* 2008; 451:480-4; PMID:18216857; <http://dx.doi.org/10.1038/nature06520>
- Gallego-Bartolomé J, Alabadí D, Blázquez MA. DELLA-induced early transcriptional changes during etiolated development in *Arabidopsis thaliana*. *PLoS ONE* 2011; 6:e23918; PMID:21904598; <http://dx.doi.org/10.1371/journal.pone.0023918>
- Hedden P, Proebsting WM. Genetic analysis of gibberellin biosynthesis. *Plant Physiol* 1999; 119:365-70; PMID:9952430; <http://dx.doi.org/10.1104/pp.119.2.365>
- Hedden P, Phillips AL. Gibberellin metabolism: new insights revealed by the genes. *Trends Plant Sci* 2000; 5:523-30; PMID:11120474; [http://dx.doi.org/10.1016/S1360-1385\(00\)01790-8](http://dx.doi.org/10.1016/S1360-1385(00)01790-8)

38. Olszewski N, Sun TP, Gubler F. Gibberellin signaling: biosynthesis, catabolism, and response pathways. *Plant Cell* 2002; 14(Suppl):S61-80; PMID:12045270
39. Sakamoto T, Kamiya N, Ueguchi-Tanaka M, Iwahori S, Matsuoka M. KNOX homeodomain protein directly suppresses the expression of a gibberellin biosynthetic gene in the tobacco shoot apical meristem. *Genes Dev* 2001; 15:581-90; PMID:11238378; <http://dx.doi.org/10.1101/gad.867901>
40. Hay A, Kaur H, Phillips A, Hedden P, Hake S, Tsiantis M. The gibberellin pathway mediates KNOTTED1-type homeobox function in plants with different body plans. *Curr Biol* 2002; 12:1557-65; PMID:12372247; [http://dx.doi.org/10.1016/S0960-9822\(02\)01125-9](http://dx.doi.org/10.1016/S0960-9822(02)01125-9)
41. Sentoku N, Sato Y, Kurata N, Ito Y, Kitano H, Matsuoka M. Regional expression of the rice KN1-type homeobox gene family during embryo, shoot, and flower development. *Plant Cell* 1999; 11:1651-64; PMID:10488233
42. Silverstone AL, Chang C, Krol E, Sun TP. Developmental regulation of the gibberellin biosynthetic gene GA1 in *Arabidopsis thaliana*. *Plant J* 1997; 12:9-19; PMID:9263448; <http://dx.doi.org/10.1046/j.1365-313X.1997.12010009.x>
43. He J X, Li Q F. Mechanism of signalling crosstalk between brassinosteroids and gibberellins. *Plant signalling behaviour* 2013; 8:7 e 2486,
44. Griffiths J, Murase K, Rieu I, Zentella R, Zhang ZL, Powers SJ, et al. Genetic characterization and functional analysis of the GID1 gibberellin receptors in *Arabidopsis*. *Plant Cell* 2006; 18:3399-414; PMID:17194763; <http://dx.doi.org/10.1105/tpc.106.047415>
45. Chhun T, Aya K, Asano K, Yamamoto E, Morinaka Y, Watanabe M, et al. Gibberellin regulates pollen viability and pollen tube growth in rice. *Plant Cell* 2007; 19:3876-88; PMID:18083909; <http://dx.doi.org/10.1105/tpc.107.054759>
46. Hu J, Mitchum MG, Barnaby N, Ayele BT, Ogawa M, Nam E, et al. Potential sites of bioactive gibberellin production during reproductive growth in *Arabidopsis*. *Plant Cell* 2008; 20:320-36; PMID:18310462; <http://dx.doi.org/10.1105/tpc.107.057752>
47. Rieu I, Ruiz-Rivero O, Fernandez-Garcia N, Griffiths J, Powers SJ, Gong F, et al. The gibberellin biosynthetic genes AtGA20ox1 and AtGA20ox2 act, partially redundantly, to promote growth and development throughout the *Arabidopsis* life cycle. *Plant J* 2008; 53:488-504; PMID:18069939; <http://dx.doi.org/10.1111/j.1365-313X.2007.03356.x>
48. Nester JE, Zeevaert J A D. Flower development in normal tomato and a gibberellin-deficient (ga-2) mutant. *Am J Bot* 1988; 75:45-55; <http://dx.doi.org/10.2307/2443904>
49. Goto N, Pharis RP. Role of gibberellins in the development of floral organs of the gibberellin-deficient mutant, gal-1, of *Arabidopsis thaliana*. *Canadian Journal of Botany-Revue Canadienne De Botanique* 1999; 77:944-54; <http://dx.doi.org/10.1139/cjb-77-7-944>
50. Koornneef M, Vander Veen JH. Induction and analysis of gibberellin sensitive mutants in *Arabidopsis thaliana* (L.) Heynh. *Theor Appl Genet* 1980; 58:257-63; <http://dx.doi.org/10.1007/BF00265176>
51. Hirano K, Aya K, Hobo T, Sakakibara H, Kojima M, Shim RA, et al. Comprehensive transcriptome analysis of phytohormone biosynthesis and signaling genes in microspore/pollen and tapetum of rice. *Plant Cell Physiol* 2008; 49:1429-50; PMID:18718932; <http://dx.doi.org/10.1093/pcp/pcn123>
52. Plack A. Effect of gibberellic acid on corolla size. *Nature* 1958; 182:610; PMID:13577927; <http://dx.doi.org/10.1038/182610a0>
53. Cheng H, Qin LJ, Lee SC, Fu XD, Richards DE, Cao DN, et al. Gibberellin regulates *Arabidopsis* floral development via suppression of DELLA protein function. *Development* 2004; 131:1055-64; PMID:14973286; <http://dx.doi.org/10.1242/dev.00992>
54. Izhaki A, Borochoy A, Zamski E, Weiss D. Gibberellin regulates post-microsporogenesis processes in petunia anthers. *Physiol Plant* 2002; 115:442-7; PMID:12081537; <http://dx.doi.org/10.1034/j.1399-3054.2002.1150314.x>
55. Goldberg RB, Beals TP, Sanders PM. Anther development: basic principles and practical applications. *Plant Cell* 1993; 5:1217-29; PMID:8281038
56. Itoh H, Ueguchi-Tanaka M, Sentoku N, Kitano H, Matsuoka M, Kobayashi M. Cloning and functional analysis of two gibberellin 3 beta -hydroxylase genes that are differentially expressed during the growth of rice. *Proc Natl Acad Sci USA* 2001; 98:8909-14; PMID:11438692; <http://dx.doi.org/10.1073/pnas.141239398>
57. Singh DP, Jermakow AM, Swain SM. Gibberellins are required for seed development and pollen tube growth in *Arabidopsis*. *Plant Cell* 2002; 14:3133-47; PMID:12468732; <http://dx.doi.org/10.1105/tpc.003046>
58. Song S, Qi T, Huang H, Xie D. Regulation of stamen development by coordinated action of Jasmonate, auxine and gibberellin in *Arabidopsis*. *Molecular plant advances*, 2013 online .
59. Barendse GWM, Rodrigues-Pereira AJ, Berkers PA, Driessen FM. Growth hormones in pollen, styles and ovaries of *Petunia* hybrid and *Lilium* species. *Acta Bot. Neerl.* 1970; 19:175-86
60. Pharis RP, King RW. Gibberellins and reproductive development in seed plants. *Annu Rev Plant Physiol* 1985; 36:517-68; <http://dx.doi.org/10.1146/annurev.pp.36.060185.002505>
61. Fuchs E, Atsmon D, Halvey AH. Adventitious staminate flower formation in gibberellin treated gynococious cucumber plants. *Plant Cell Physiol* 1977; 18:1193-201
62. Pimenta Lange MJ, Knop N, Lange T. Stamen-derived bioactive gibberellin is essential for male flower development of *Cucurbita maxima* L. *J Exp Bot* 2012; 63:2681-91; PMID:22268154; <http://dx.doi.org/10.1093/jxb/err448>
63. Galun E. Effect of gibberellic acid and naphthaleneacetic acid on sex expression and some morphological characters in the cucumber plant. *Phyton* 1959; 13:1-8
64. Kubicki B. Investigation of sex determination in cucumbers (*Cucumis sativus*). The influence of 1-naphthalene acetic acid and gibberellin on differentiation of flowers in monoecious cucumbers. *Genet.Pol.* 1965; 6:153-76
65. Banarjee S, Basu PS. Hormonal regulators of flowering and fruit development: effect of GA and ethereal on fruit setting and development of *Momordica charinata* L. *Biol Plant* 1992; 34:63-70; <http://dx.doi.org/10.1007/BF02925792>
66. Nagmani S. Studies on crop growth and sex expression in relation to hybrid seed production of bitter gourd (*Momordica charinata* L.) M.Sc. thesis submitted to Faculty of Post Graduate Schol, IARI, New Delhi., 2011.
67. White CN, Proebsting WM, Hedden P, Rivin CJ. Gibberellins and seed development in maize. I. Evidence that gibberellin/abscisic acid balance governs germination versus maturation pathways. *Plant Physiol* 2000; 122:1081-8; PMID:10759503; <http://dx.doi.org/10.1104/pp.122.4.1081>
68. Jacobsen JV, Pearce DW, Poole AT, Pharis RP, Mander LN. Absciscic acid, phaseic acid and gibberellin contents associated with dormancy and germination in barley. *Physiol Plant* 2002; 115:428-41; PMID:12081536; <http://dx.doi.org/10.1034/j.1399-3054.2002.1150313.x>